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Southern Hemisphere Humpback Whale Song in Pacific Central America

First Description of the Song of Costa Rica, Pace of Song Change over Time,
and the Impacts of Engine Noise on Acoustic Activity



An Honors College Thesis

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Abstract

The humpback whale (*Megaptera novaeangliae*) is a species of marine mammal famed for its charisma and song. This thesis focuses on the population of whales that feeds in the Pacific waters off the coast of Chile and the Antarctic Peninsula and breeds in the Pacific waters off the coast of Ecuador and Central America, which constitutes a poorly known breeding ground. Studies have previously shown that these whales are capable of cultural transmission, which is to pass on song elements over space and time, allowing scientists to track them around the world. Cultural transmission implies acoustic contact and can assist in establishing migratory routes and population overlaps. This thesis has 3 distinct studies which have been segregated by chapters. The first and last chapters of this thesis serve as an introduction and conclusion respectively. In chapter 2, I describe the average breeding song of 2016 of Costa Rica using data collected with autonomous hydrophone recorders. I found 14 phrases grouped into 4 themes. This song changed over the season and varied between individuals, consistent with other studies. In chapter 3, I describe the pace of song change between the period of 2007-2017 using data collected in Panama and Costa Rica. The pace of change increased over this period, suggesting that this population is not acoustically isolated. In chapter 4, we examine the effects of engine noise of acoustic behavior. We find that whales are significantly more quiet in the presence of engine noise. In countries where ecotourism is present, like Costa Rica, the education of boat drivers and fishing industry is imperative to the preservation of this species. Countries fortunate enough to have these creatures call their waters home have an obligation to protect them against anthropogenic threats through education and the implementation of eco-friendly policy.

Key Words: acoustic communication; conservation; cultural transmission; engine noise; humpback whale; song; song description.

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Chapter 1: Introduction

Background and Literature Review

The humpback whale (*Megaptera novaeangliae*) is a species of marine mammal famed for its beauty and charisma (Fig.1). This baleen whale is the only species in the genus *Megaptera* (Fig.2). Humpbacks are anatomically and behaviorally distinct from other mysticete whales due to their long pectoral fins, the presence of tubercles, and their active surface behavior. These tubercles are large, round protuberances on the head, each with a single vibrissa (hair). Fossil records indicate that cetaceans evolved from *Artiodactyla* (i.e. even-toed hoofed mammals, such as the hippopotamus) roughly 50 million years ago when this group first began to inhabit an aquatic environment. Mysticete (baleen) whales began to diverge from Odontocete (toothed) cetaceans roughly 33 million years ago. *Megaptera* is a relatively more recent genus with fossil records indicating an origin in the Pliocene epoch (< 5 Mya) (Sasaki et al. 2005). The humpback whale is today the only species in this genus.

Today, the humpback whale has one of the largest geographical ranges in the animal kingdom coupled with a strong annual cycle; summering in prey-abundant high latitude waters and then migrating to tropical waters in the winter to breed and give birth, performing one of the most impressive migrations of any animal (Rasmussen *et al.* 2007). There are currently 14 established breeding grounds recognized by the National Oceanic and Atmospheric Administration, constituting distinct population segments (DPS) (Fig.3).

Humpback whales lack a cohesive social structure, preferring instead to remain in small, unstable groups that only reside together for a few hours on average. (Clapham et al. 1992) While in the high latitude feeding grounds, these groups generally tend to reflect the distribution of locally

abundant prey. During the breeding season, the most common social unit is the mother-calf pair, which forms the most stable and cohesive social group in the humpback whale social system. The mother will remain with the calf for roughly one year before parting ways. The second most stable structure is that of the mother-calf-escort group. This group consists of a mother and calf accompanied by a principal escort. Escorts have been determined to be male humpbacks that guard mother-calf pairs (Darling et al. 1983; Clapham et al. 1992). The leading theory is that these males attempt to copulate with these females and is an example of mate guarding. Escorts generally do not tend stay with mother-calf pairs longer than a few days (Baker & Herman, 1984). Another less stable social group is the competitive group. Males will often congregate to form a competitive group that tends not to last for more than a few hours and consists of males competing for access to females (Tyack & Whitehead, 1983; Clapham et al. 1992).

One of the most famous characteristics of the humpback whale is its song. Acoustics are paramount to the social structure of cetaceans, including humpback whales. (Tyack & Miller, 2002) It is on the breeding grounds that male humpback whales sing their incredibly beautiful and complex songs, the hierarchy of which consists of units, phrases, and themes. (Payne & McVay, 1971). These songs have a frequency range of 100Hz to 4kHz (Tyack & Clark, 2000), with harmonics sometimes reaching up to 24kHz (Au et al. 2006). While hearing in humpbacks has been largely unstudied, it is generally accepted that species can hear calls produced by their own species, suggesting that humpbacks can hear between 100Hz and 4kHz. The typical low frequency of these songs means that they can travel for hundreds of kilometers, allowing humpbacks to stay in contact over long distances. The purpose of the stereotypical song has been largely debated. There are currently four main hypotheses which attempt to explain the function of male humpback

song: (1) to attract females to individual males (2) to mediate male-male interactions (3) to attract females to a lek (as reviewed in Herman, 2016) and (4) as sonar (Mercado et al. 1996).

The first hypothesis suggests that males sing to attract sexually mature females to copulate. However, this hypothesis lacks empirical evidence. For example, playback experiments in which a song was projected via an underwater speaker attached to a stationary boat conducted by Tyack (1983) and Mobley et al. (1988) were unable to support this hypothesis as no known females approached the source of the song. Extensive observational studies have also shown that females do not approach singers. Despite a lack of evidence to suggest that females are approaching lone male singers, it is possible that females are signaling to these males through surface activity such as pectoral slapping. A study by Deakos et al. (2002) provided evidence that group turnover (i.e. affiliations and disaffiliations of males from the pod) occurred more often when percussive sounds were more frequent. This does provide evidence of female choice, without the necessity of directly approaching a lone signing male. However, I do not believe that these female behaviors are in response to song, as surface activity was observed in the presence of other males, and not as a direct response to singing, which usually occurs when a male is solitary, as evidenced by playback experiments. Herman, in his 2016 review paper, emphasizes the fact that the complexity of male song itself could be evidence to support the female choice hypothesis as females could potentially use cues in the song as insights to male fitness, although this has not been tested.

The second hypothesis states that male song functions as a mediator in male-male interactions to minimize physical conflict on the breeding grounds through either dominance hierarchies or alliance formation. However, Darling & Bérubé (2001) could find no support for the use of song to establish dominance hierarchies. They noted that given the ephemeral nature of most humpback interactions, these whales would have to possess the capacity to remember and

recognize numerous individuals into the future, which seems unlikely. It should be noted that they observed that singing males typically fall silent when approached by other males, an act which could be considered aggressive as it disrupts a display. In the absence of dominance hierarchies, song could still potentially function as a conflict mediator. Cholewiak et al. (2018) described how males increase the evenness of their songs in the presence of other males as well as the rate at which they switch between different phrases, suggesting that this behavior allows rival males to assess one another more completely. This behavior has been demonstrated in song birds to be a low-level agonistic behavior. The authors also provide evidence of song type matching, which allows males to direct song towards a specific male, indicating an aggressive behavior. In reference to non-agonistic behavior, or alliance formation, there have been observational studies that cite males working cooperatively in competitive groups and leaving the group together (e.g. Tyack & Whitehead, 1983). However, it was noted in Darling et al. (2006) that many of these associations were formed without singing observed before-hand. Therefore, it can be suggested that alliances are formed through prior associations rather than by singing to attract a potential alliance member.

The third hypothesis states that male song functions as a lek, attracting females to the warmer waters of the breeding ground (Herman & Tavolga, 1980). The breeding grounds fit the definition of a lek because males display in these areas and there are no resources in this area for non-gravid females other than potential mates, as prey is extremely scarce in these areas. It is also suggested that females do indeed make mate choices, as females are typically larger than males. Even though males do not establish permanent geographic territories, Clapham (1996) defined the “floating lek”, which signifies an acoustic territory whose location is plastic, rather than an established permanent geographic location on the breeding grounds. This allows the lekking hypothesis to be retained in this mating system. Höglund & Alatalo (1995) noted that females are

more likely to approach larger groups of singing males than a lone male and thus it can be inferred that males who participate in aggregations are more successful than those who do not. From this information as well as other studies, it can be inferred that the humpback whale breeding system follows a lekking model.

The fourth hypothesis states that male song functions as sonar (Mercado et al. 1996). These authors have discussed over various publications the viability of this hypothesis. It is suggested that songs function as sonar in the sense that humpbacks can locate one another by listening for the echoes of their songs. They cite the ability of males to find non-vocalizing females as evidence for the sonar model, along with the spacing of singers (4km-6km) at the upper limits of their sonar detection range (Frazer & Mercado, 2000). In the teams' 1996 and 2000 papers, they discuss that all mammals have some ability to "echo-locate" if not only to corroborate other sensory information. The idea that mysticetes do not echolocate is therefore incorrect, they simply do not echolocate with the precision and the stereotypical high-frequency sounds of some odontocetes, such as bottle-nosed dolphins. The authors acknowledge that intersexual selection may play a secondary role in the song's function, assisting in explaining some of the complexity of the song. Yet, this would not account for the vast and complicated vocal repertoire ascribed to humpbacks as well as the observed cultural transmission of songs. Further, since hearing in mysticetes is relatively unstudied, I feel that more studies need to be done to determine the validity of this hypothesis.

Songs can vary between individuals as well as seasons (Payne et al., 1983; Payne & Payne, 1985). However, males will generally conform to the songs of their conspecifics, resulting in the relatively same song. Song can also be used to monitor populations and migration routes as specific regions will have distinct songs, allowing scientists to "track" these songs globally using acoustic

monitoring (Winn et al. 1981; Noad et al. 2000; Garland et al. 2011). This allows scientists an efficient and cheap way to monitor these populations, which is of the utmost importance in the light of increasing anthropogenic threats.

Today, these creatures face numerous anthropogenic threats, such as lowered genetic diversity caused by whaling, noise pollution, collision with large shipping vessels, and prey degradation. Although the humpback whale population has been increasing since the 1966 moratorium on whaling, it is still necessary to understand the threats these animals still face to preserve the species.

Historically, many cultures have long revered these whales as deities, believing that sighting a whale was a symbol of good luck and prosperity. Whales were often a source of sustenance for early tribal communities, with one whale providing an entire village with enough provisions for the whole winter. However, the development of larger shipping vessels with stern slipways and more advanced weaponry, such as the exploding harpoon, by the end of the 1800's signaled the beginnings of commercial whaling and thus the decimation of the global humpback whale population. The first formal studies of these magnificent ocean dwellers were conducted in association with commercial whaling, such as studies of migration using "discovery tags". Scientists aboard these vessels would tag whales with ID's later returned to them by the whalers if the whale was later caught. The once rich population of humpback whales was reduced to 90% of its original number, prompting a 1966 moratorium on humpback whale hunting declared by the International Whaling Commission. Since then, the population has rebounded but has never regained its pre-commercial whaling numbers, thus making the conservation of these animals a top priority. Further, humans have also extensively exploited the prey populations of these animals and increasing noise pollution further degrades these animals' marine habitat. Collision with larger

shipping vessels and entanglement in fishing nets have also increased the mortality of the humpbacks. Because of these relatively recent anthropogenic threats to the humpback whale population, it should be noted that the conditions under which humpback whale behavior has evolved are largely different than those observed today.

Today, the humpback whale population is increasing overall, with only 1 distinct population segment deemed at high risk (Bettridge et al. 2015). Even though the global population of humpbacks is increasing, they still face many anthropogenic threats, such as noise pollution.

Due to their beauty, charisma, and predictability, these animals have become an important tourist attraction in this area, leading to an increasing number of boats dedicated to whale-watching activities. Exposure of coastal populations of marine mammals to increasing levels of noise pollution is generating concern in the scientific community. This concern is founded in the masking potential of engine noise on acoustic communications. Since boat engines do not have mufflers to reduce noise output, these whale-watching vessels have the potential to change the acoustic space of these animals and indirectly affect their breeding success. Acoustic communication is extremely important for humpback whales and indeed for many other marine mammals as it plays an integral role in socializing and reproducing (Weilgart, 2007). This is especially worrying when engine noise is directly targeted at these animals, as is the case with whale watching boats.

Sound travels with ease underwater and therefore the area impacted by engine noise can reach upwards of millions of cubic kilometers. This fact is of special concern for cetaceans, as they rely on acoustics as their primary sense and method of communication (Tyack & Miller, 2002). Ocean background noise has doubled every decade for the past several decades, which is most likely due to the increase in commercial shipping (McDonald et al. 2006). The increased use of

naval sonars is also cause for concern as these extremely loud blasts of noise have been connected to beaked whale strandings dating back to 1991 (Simmonds & Lopez-Jurado, 1991). While these strandings can be fatal, other chronic effects are also cause for immediate concern. These effects include increased stress levels, abandonment of important breeding habitat, masking, and changes in diving behavior (Weilgart, 2007). A study conducted on the effects of whale watching boats on killer whales suggests that these boats can even contribute to both short term and permanent hearing loss (Erbe, 2002).

Several studies suggest that there is a negative correlation between number of boats and number of actively singing humpback whales (Risch et al. 2012; Sousa-Lima & Clark, 2008; Stamation et al. 2010). The data collected in these studies suggest that in the presence of anthropogenic noise, humpback whales will go silent, stay submerged for longer periods of time, and will expend energy to move further away from these vessels.

Thesis Goals

The objective of this thesis is to more fully understand the acoustic behavior of these whales in a poorly known breeding ground. This thesis will work with acoustic data gathered in Costa Rica and Panama between 2007 and 2017. This thesis has 3 major goals outlined below:

1. To describe for the first time the breeding song of Pacific Costa Rica in 2016
2. To quantify the pace of song change over the period of 2007-2017 in Pacific Central America
3. To determine the effect of engine noise on the acoustic behavior of these whales

This thesis is a part of the larger Project Ondas (PI: Dr. Laura May-Collado) which seeks to gather research on cetaceans in Central America to better inform policy regarding the protection of these animals. It is the overall goal of this thesis to provide original information to the scientific

community regarding this population of whales so that they may be better understood and protected.

It should be noted that I use the word “we” later in this thesis, this refers to myself and my peers who generously assisted me in analyzing the vast amount of data.

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Figures

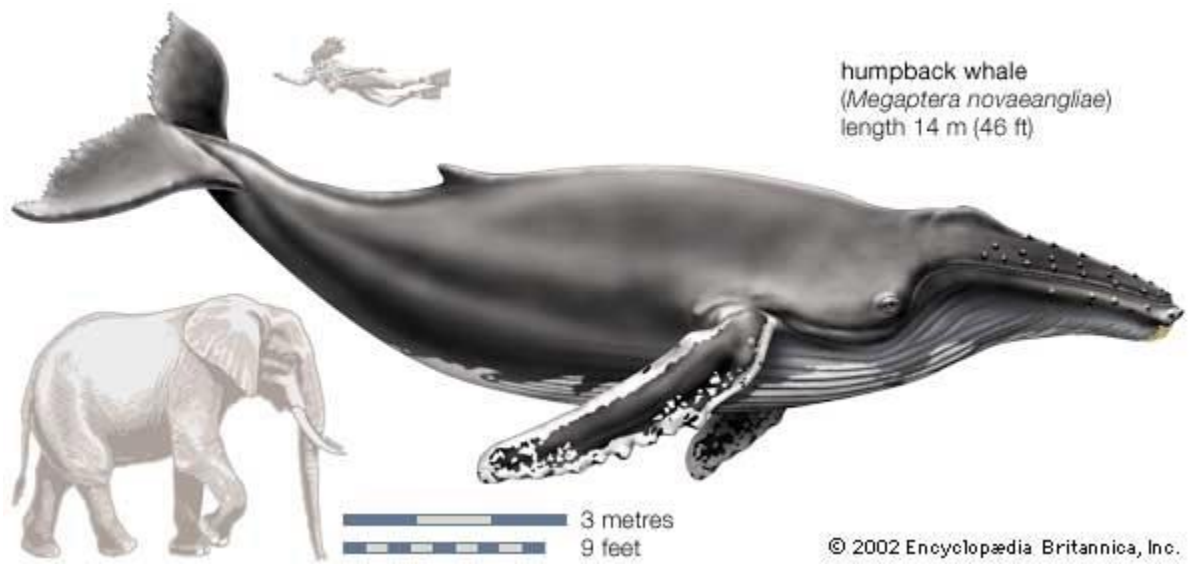


Figure 1. A humpback whale (*Megaptera novaeangliae*) displayed alongside a human and elephant to illustrate scale.

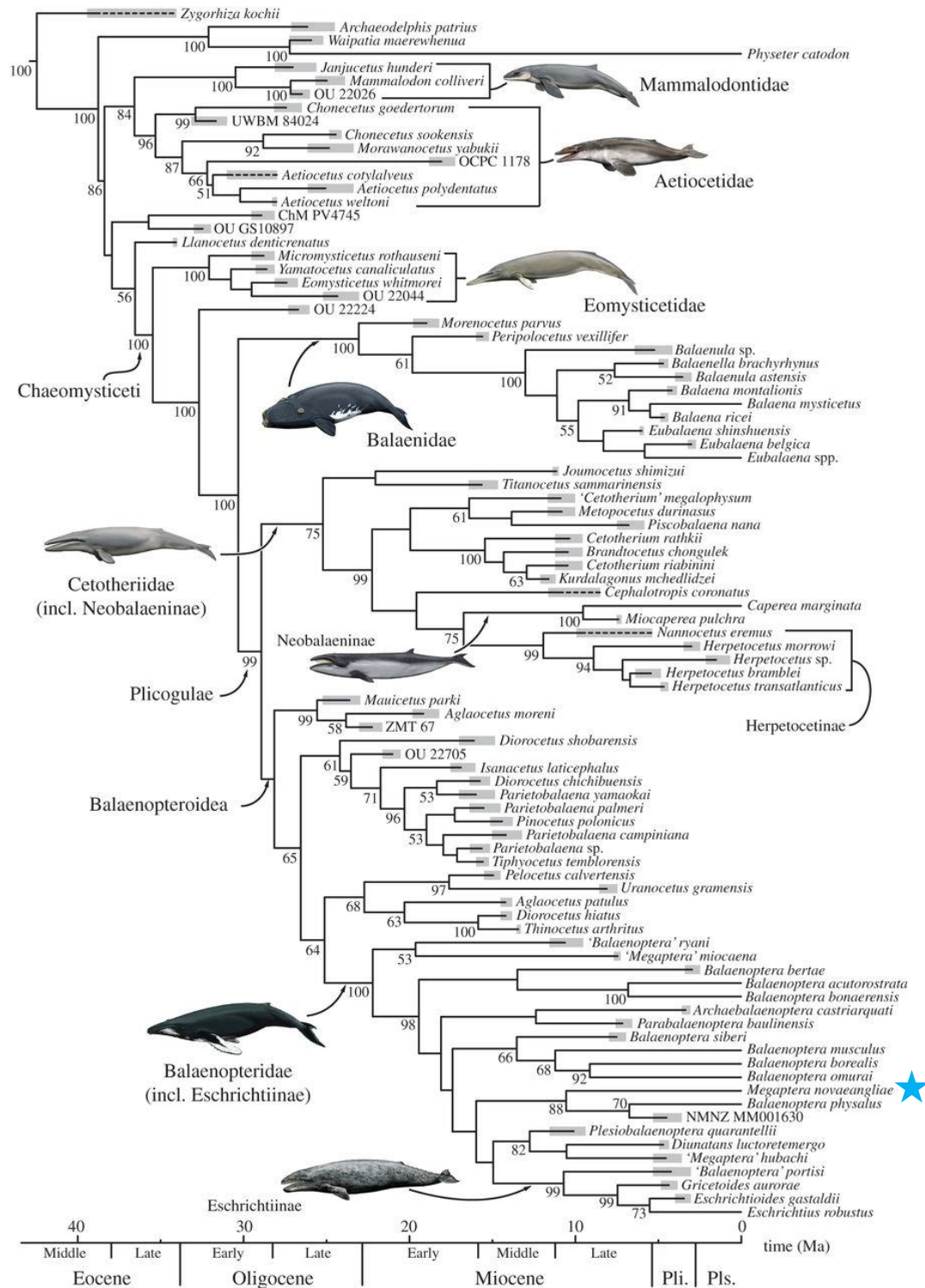


Figure 2. A phylogenetic tree illustrating the evolutionary relationships of baleen whales using both morphological and molecular data (Marx & Fordyce, 2015). Humpback whales (*Megaptera novaeangliae*) are denoted with a blue star.

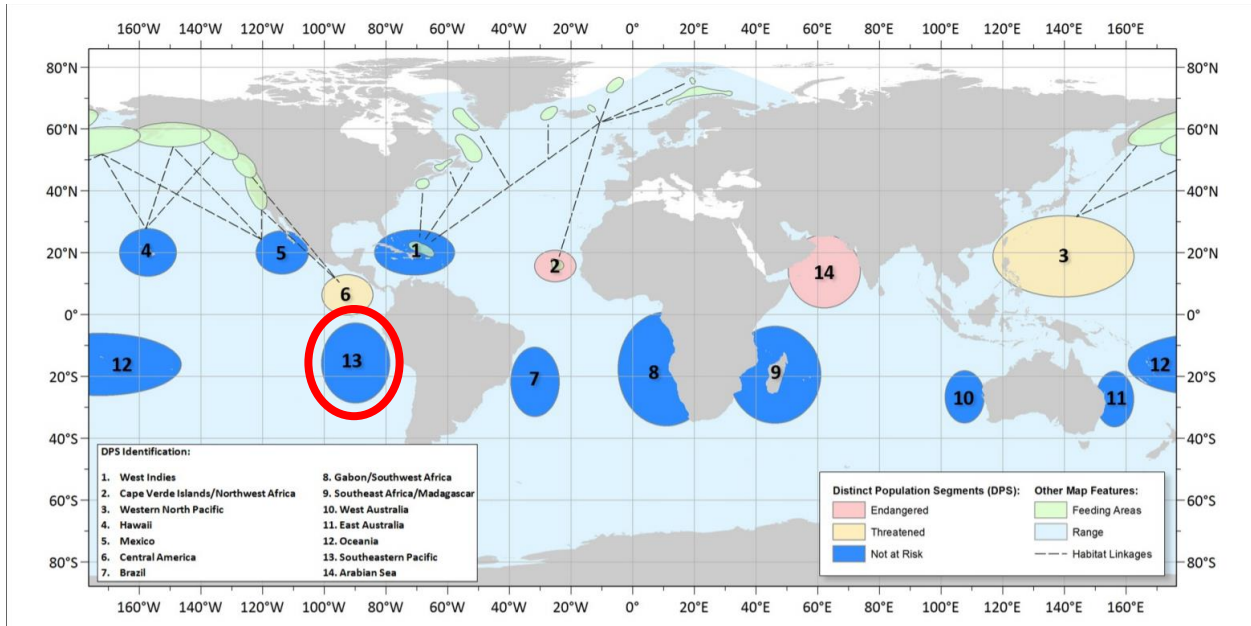


Figure 3. A map illustrating the DPS formally recognized by NOAA in 2016. The population of focus in this thesis has been noted by a red circle.

Chapter 2: Description of 2016 Song of Pacific Costa Rica

Abstract

During the breeding season, humpback males will sing their characteristic songs. It is accepted that these songs are subjected to variation at the individual, seasonal, and yearly levels. This study seeks to describe the humpback song of 2016 in Costa Rica through the further development of less subjective classification guidelines. This song had 13 unique units, 14 phrases, and 4 themes. Seasonal variation was demonstrated through the addition of 2 new phrases and loss of 3 phrases half-way through the season. This was also shown through changes in the most common phrase for theme I over time. Despite these changes, theme order remained relatively consistent, with only 3 out of 16 singers analyzed varying from the average theme order. Describing humpback songs in detail will facilitate easy cross comparison between populations, potentially giving insights to population structure and overlap.

Key words: humpback whale, song description, classification guideline, seasonal variability

Introduction

While on their low-latitude breeding grounds, male humpback whales (*Megaptera novaeangliae*) will sing their characteristic songs. While there is dispute in the scientific community, it is generally accepted that these songs serve as an attractant to females. Songs can vary between individuals as well as seasons (Payne et al. 1983). It is accepted that separate populations will sing distinctive songs, with similarity being associated with the geographic distance between 2 given populations (Winn et al. 1981; Payne & Guinee, 1983; Noad et al. 2000). Therefore, establishing song structure for a given region will facilitate easy comparisons between other populations and could provide insights into cultural transmission between populations. The

goal of this study is to describe the structure of the 2016 humpback whale song for the Southern Hemisphere population of whales wintering in Costa Rica.

This breeding ground was first described by Acevedo & Smultea (1995) and it was later established that these whales feed in the area surrounding the Antarctic Peninsula and the Magellan Strait (Rasmussen et al. 2004; Acevedo et al. 2007). Genetic evidence suggests that these whales overlap with the Northern Hemisphere whales that feed off the Pacific coast of the U.S. while on the breeding grounds (Baker et al. 1993; Baker et al. 1998; Medrano-Gonzalez et al. 2001). An observational study has also reported an instance of a whale moving between the Pacific and Atlantic populations of South America, suggesting flow between these two geographically distinct populations (Stevick et al. 2013). These genetic and observation studies imply that acoustic transmission might also be taking place, emphasizing the significance of describing the song of this region to add another layer of analysis to the movements of this population.

When first described in 1971 by Payne & McVay, the male humpback whale song was classified into a hierarchical system consisting of subunits, units, subphrases, phrases, themes, songs, and song sessions, listed in ascending order. These definitions were often subjective, with phrases referred to as “stereotyped patterns” and themes listed as simply “similar” groupings of phrases (e.g. Cerchio et al. 2001; Garland et al. 2011; Cholewiak et al. 2013).

Recently, Cholewiak et al. (2013) provided a historical discussion of the problems of classification of humpback whale song and suggested methods to reduce subjectivity when classifying songs. Despite this effort, the authors do acknowledge that their suggestions may not function universally. This chapter will further develop the current classification guidelines in the hopes of further eliminating subjectivity to produce quantifiable definitions, while simultaneously describing the song of 2016 of Costa Rica.

Methods

I. Study Site

Southern Hemisphere humpback whale song recordings were obtained from Isla del Caño Biological Reserve (8.715060, -83.870927) in 2016 (Fig.1) using interchangeably two autonomous underwater recorders RUDAR-mk2 (Cetacean Research Technology, Inc.) and SM2M+ (Wildlife Acoustics) The recorders were programmed to record continuously for 10-15 days at sampling rate of 48 kHz. Table 1 shows the effort per month and recorder model while Table 2 displays the effort of this study. Estimations from the RUDAR manufacturers that the detection range for humpback whales on good weather conditions is likely between 10 and 20 km.

II. Data Collection

I classified the song structure of this area in 2016 using the descriptions outlined in Table 3. Recordings used in analysis were separated by 24 hours to minimize the risk of sampling the same whale twice. Only recordings with visible harmonics were used to ensure quality analysis. From these recordings, only samples that had at least 1 full song cycle by a single whale were used in the final analysis. All songs were analyzed manually using Raven 1.5 (2016; Cornell Lab of Ornithology) with a fast Fourier transform size of 2,048 points, an overlap of 50%, and a 512-sample Hann window. Units were first established, followed by phrases, and themes. Subunits were not identified. All phrases were then counted and averaged to calculate the average phrase count per hour of recording as some recordings were longer than others. To calculate the proportion of an hour dedicated to a specific phrase, the phrase counts were then divided by total phrase counts. The phrase counts per hour were then grouped into their respective themes. To calculate proportion of an hour dedicated to a specific theme, the sum phrase counts of a specific theme were divided by total phrase count.

Results

A total of 1030 minutes and 64 full songs were analyzed (Table 2). A total of 13 unique units were identified, along with 14 distinct phrases, and 4 themes (Fig.2, Fig.3). The most common phrase throughout the season was C with an average of 50.85 uses per hour (Table 4). Only phrases B, C, D, and K were used by 100% of singers analyzed (Fig.4). Over the course of the season, it was evident that phrase A was “replaced” by phrase M, both belonging to theme I (Fig.3). The average song had less component phrases by the end of the season, yet still followed the same theme pattern. In the last half of the breeding season analyzed, 2 new phrases, M and N, were present as well as 1 new unit, 13, demonstrating change in the average song over the course of the breeding season. The most common theme was theme I, accounting for a total of 37.9% of an average hour (Fig.5). 13 out of 16 singers adhered to the theme order of I, II, III, IV, while the other three singers were documented as singing I, II, III, I, II, III, IV. Therefore only 18.75% of singers varied from the average theme order.

Discussion

The 2016 song displayed relative adherence to the theme order of I, II, III, and IV. While there was individual variation between songs as well as change throughout the season, the theme order remained relatively constant, with only 18.75% of singers showing varied theme orders. Addition of 2 phrases and 1 unit and the loss of 3 phrases half-way through the breeding season demonstrates seasonal variability. However, seasonal and individual variation is consistent with the findings of Payne et al. (1983). Further analysis at the individual level would perhaps provide more insight into the changes that occurred over the course of the season.

Using the further developed classification guidelines described in Table 1, the average song for 2016 was described successfully. The elimination of the subphrase did not affect the

classification of the breeding song of 2016, suggesting that elimination of the subphrase should be adopted as a standard classification guideline. The new definition of “phrase” assisted in reducing subjectivity as well as making phrase classification more efficient. 2 laypersons could identify the same phrases using the guidelines established in Table 1, suggesting that the new definition is efficient and less subjective. The use of transitional phrases as guidelines for delineating themes proved to be very useful. “Similarity” is extremely subjective and it is often difficult to compare song description reports given that scientists sometimes disagree on theme delineation. The use of transitional phrases reduced subjectivity, although did not completely eliminate it. Transitional phrases were not always present and therefore the use of similarity and dissimilarity to establish themes should be maintained.

Establishing a common methodology for song classification is vital for cross-comparison. Song similarities imply that populations have recently been in acoustic contact and therefore comparing song similarities between populations is an efficient method in to examine migration routes, breeding site fidelity, and contact with other populations. Comparing songs across studies is important for conservation efforts as it can lead to more comprehensive policies.

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Figures and Tables



Figure 1. Map indicating the study area in Costa Rica where the recordings were gathered in 2016.

Table 1. Total times recorded per hydrophone in Isla del Caño in 2016.

Recorder	Recording Dates	Total time recorded (min)
SM2M+	September 19 to October 4, 2016	24,910
		45,820
Rudar-mk2	October 4 to 14, 2016	14,600
	October 24 to November 6, 2016	17,540
		32,140
Total		160,230

Table 2. Total times analyzed per date with the number of full songs per sample.

Date	Length sampled (min)	Full Songs
21-Sep	190	11
23-Sep	90	5
26-Sep	35	3
27-Sep	40	2
2-Oct	65	5
4-Oct	30	2
6-Oct	90	6
11-Oct	70	4
13-Oct	70	5
25-Oct	30	2
28-Oct	40	3
29-Oct	60	3
31-Oct	30	2
1-Nov	100	8
3-Nov	60	2
5-Nov	30	1
Total	1,030	64

Table 3. A comparison of definitions of humpback whale song hierarchical components and modifications made in this study to generate a more quantitative description of the song structure for southern humpback whales wintering in the south pacific coast of Costa Rica. For spectrograph examples of the definitions used in this study see Appendix.

<i>Song component</i>	<i>Payne and McVay (1971)</i>	<i>Payne et al. (1983)</i>	<i>Payne & Payne (1985)</i>	<i>Cholewiak et al. (2013)</i>	<i>This study</i>
<i>Subunit</i>	pulses when viewed in a spectrogram at a slower speed than real time			Points of inflection in a unit	Use Cholewiak et al.
<i>Unit</i>	shortest sound that is continuous to the human ear when played in real time	-	-	-	Definition retained
<i>Subphrase</i>	-	A series of one or more units sometimes repeated in a series.			Abandonment of the use of “subphrase”.
<i>Phrase</i>	A grouping of subphrases	-		Should be organized to minimize “hanging subphrases”	Smallest grouping of repeated units organized to minimize “hanging units”. For multiyear comparisons a new phrase therefore will consist of new units.
<i>Transitional phrase</i>	-	-	Combine units from 2 different phrase types (1985)		A group of units that represents a mixture of the phrases before and after it, is not repeated one after another, and can be used to delineate themes.

<i>Theme</i>	A series of similar phrases	Definition clarified to emphasize subphrase structure	Repetition of various similar phrases within a period of time, sometimes delimited by the presence of one or several transitional phrases.
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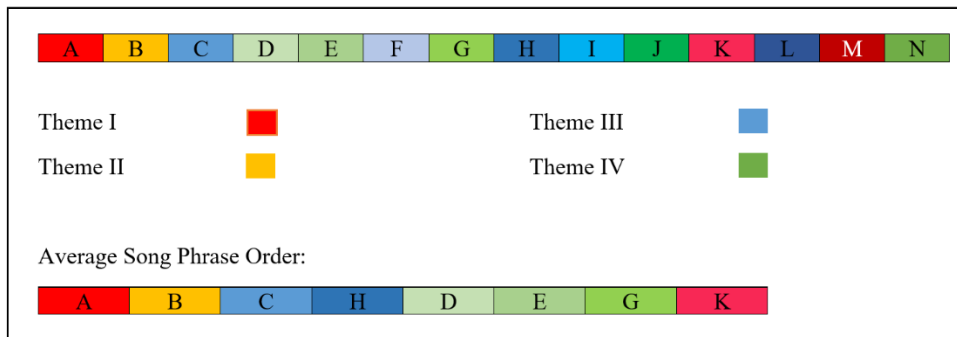


Figure 2. Phrases of the 2016 song for humpback whales in Isla del Caño, CR. Phrases are color coded by theme. Phrases are then ordered according to the average song for 2016. The blocks do not represent the proportion of one phrase to another.

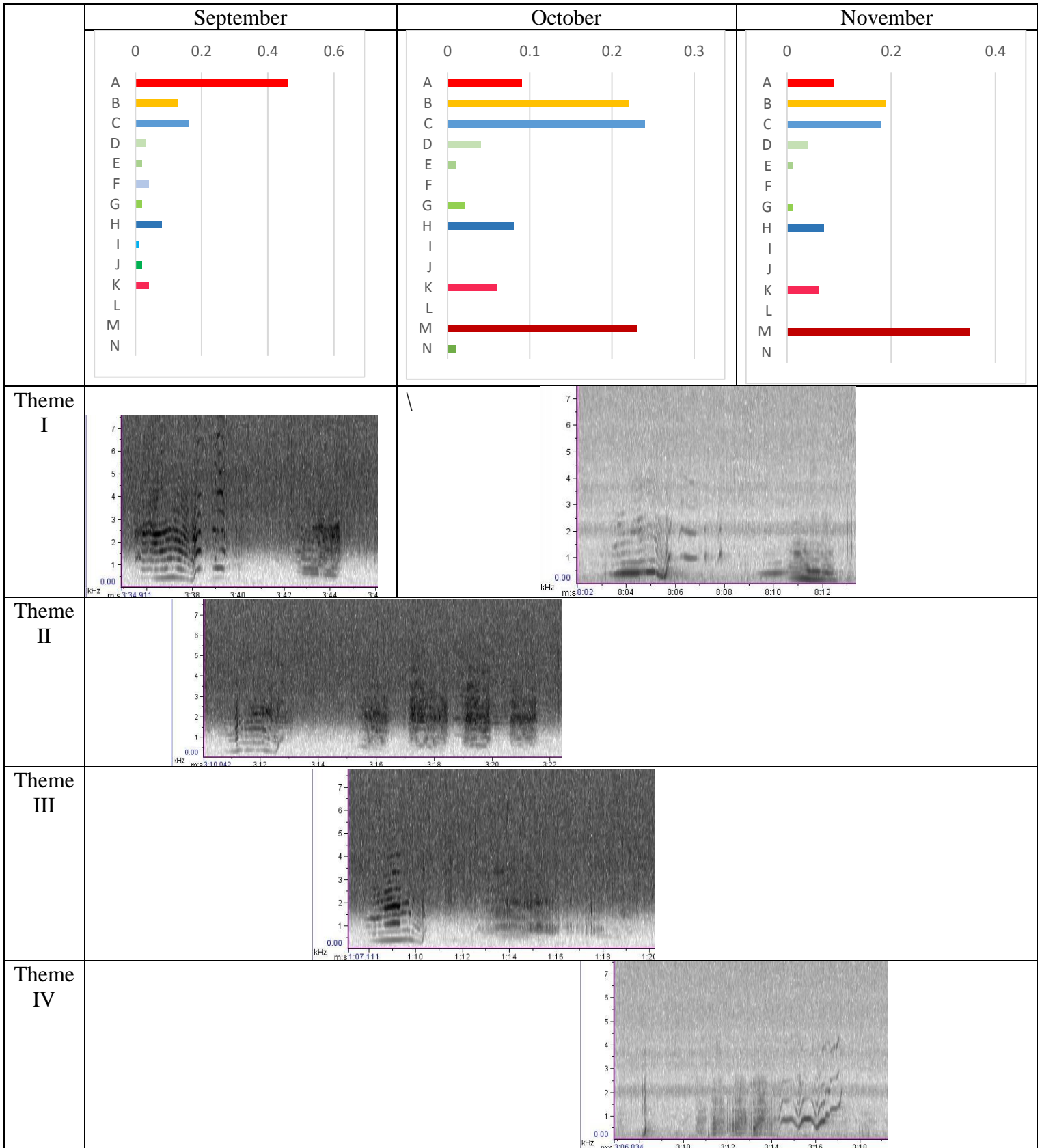


Figure 3. Average phrase proportion of song depicted by month. Spectrographs depict the most common phrase of themes I-IV for each month. Theme I-September shows phrase A and Theme I-October/November shows phrase M. The most common phrases of themes II-IV did not change over time, as depicted by merged cells. Theme II shows phrase B, theme III shows phrase C, and theme IV shows phrase D. For September, N = 4 singers, for October, N = 9 singers, for November N = 3 singers.

Table 4. Descriptive statistics for every phrase present in the 2016 song. Means reflect the average phrase count per hour.

	<i>A</i>	<i>B</i>	<i>C</i>	<i>D</i>	<i>E</i>	<i>F</i>	<i>G</i>	<i>H</i>	<i>I</i>	<i>J</i>	<i>K</i>	<i>L</i>	<i>M</i>	<i>N</i>
<i>Mean</i>	47.29	47.20	50.85	8.62	3.72	2.86	4.21	19.78	0.43	1.22	12.53	0.11	42.37	1.00
<i>SD</i>	57.56	17.21	17.99	2.34	3.16	8.19	4.15	12.96	1.65	3.07	4.43	0.41	44.88	3.87
<i>Max</i>	182.25	78.83	94.00	13.49	12.70	31.76	12.93	44.98	6.81	11.99	20.99	1.71	126.00	16.00
<i>Min</i>	0.00	17.19	24.00	4.00	0.00	0.00	0.00	0.00	0.00	0.00	3.57	0.00	0.00	0.00

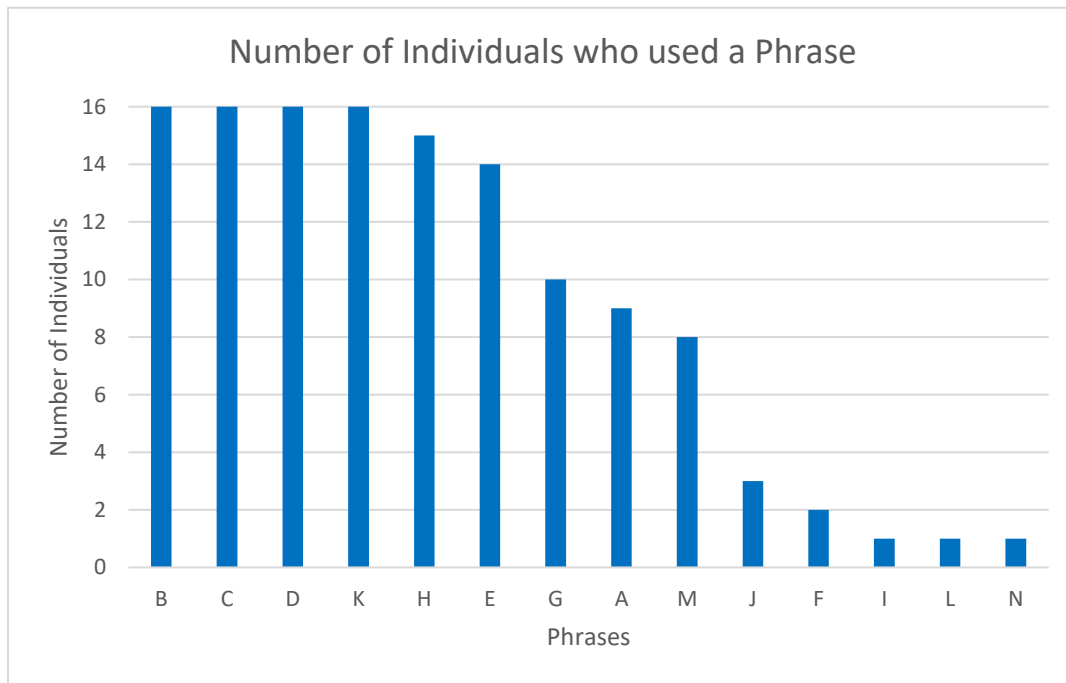


Figure 4. The percent of singers who used a phrase in the 2016 song. N = 16 individuals.

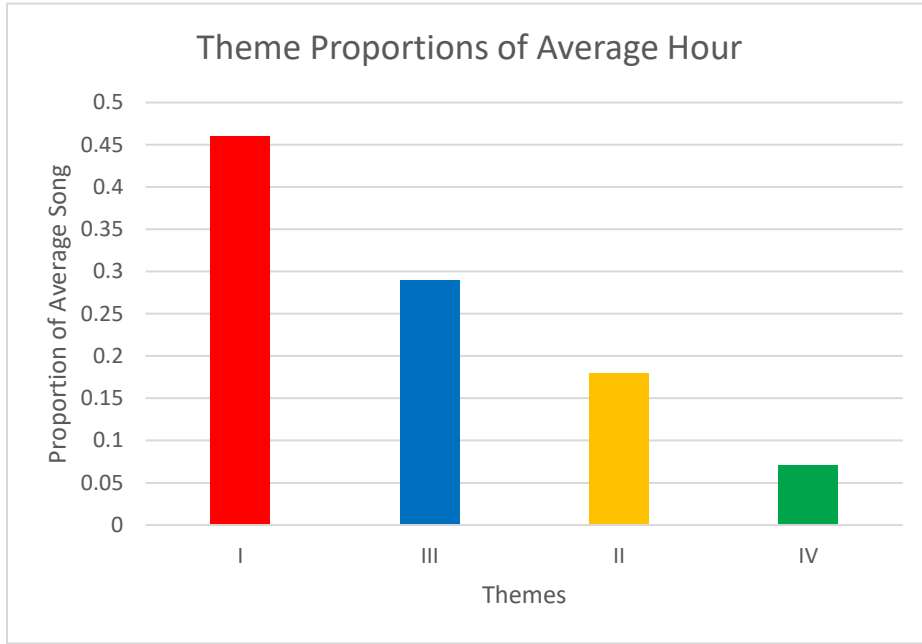
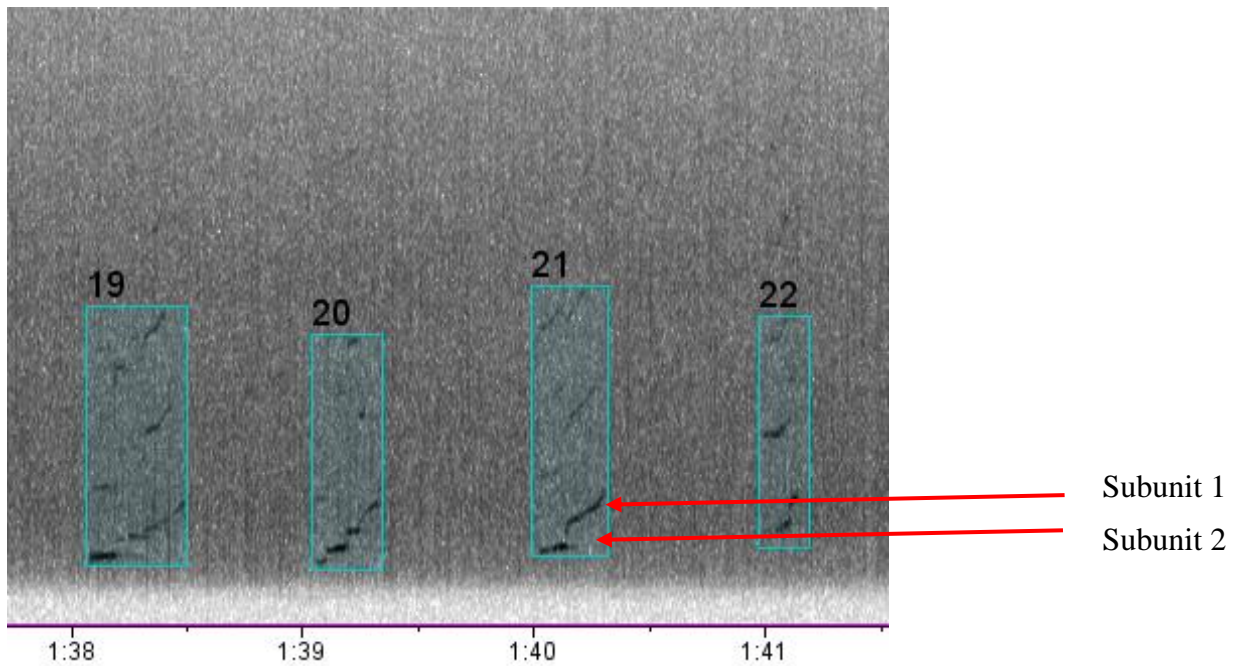


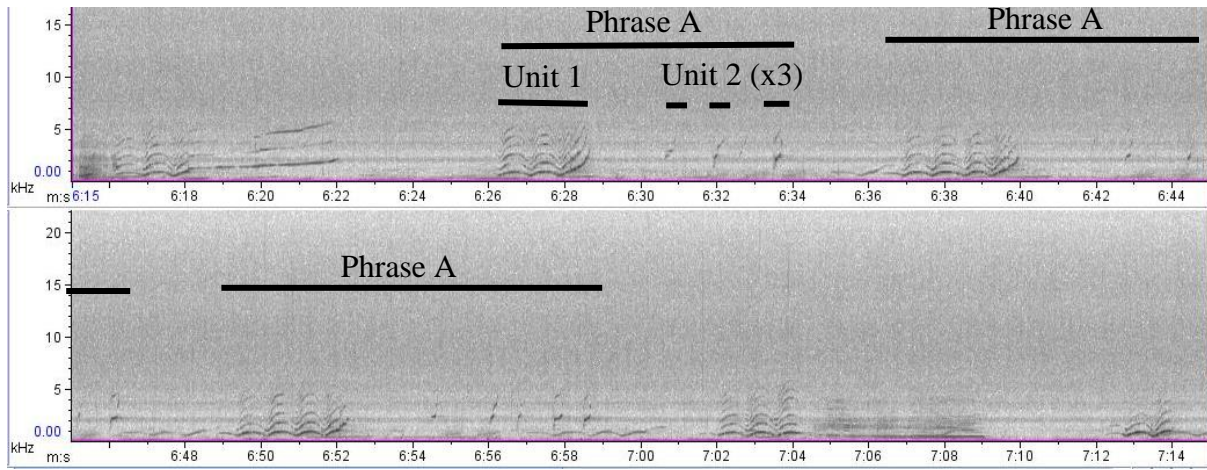
Figure 5. The average proportion of a theme in the average hour during the 2016 breeding season in Costa Rica.

Appendix

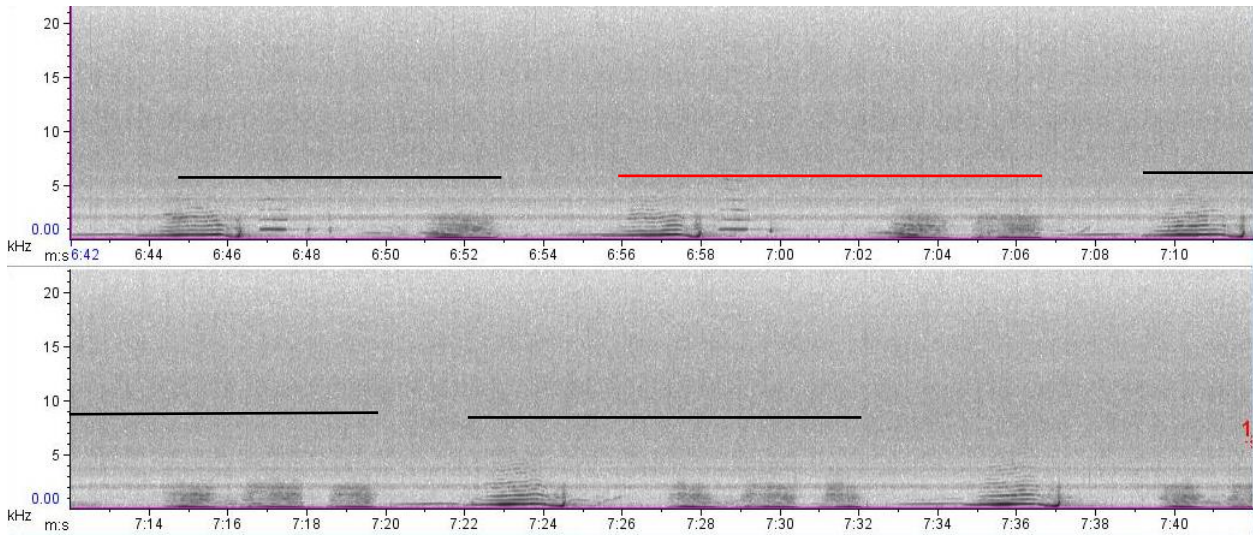
Subunit:



Unit and Phrase:



Transitional Phrase and Theme Delineation: transitional phrase shown in red and represents the delineation between two themes.



Chapter 3: Pace of Song Change Over Time

Abstract

While on their low-latitude breeding grounds, male humpback whales will sing presumably to advertise to females and (or) males. Individual males sing a series of units in a predictable order, and while their songs composition progressively changes over time, ultimately all males in a breeding population end up singing the same version of a song. This provides the means to understand humpback whale movement patterns and connectivity among populations. Here, I study the temporal changes in song structure of humpback whales from the Southern Hemisphere that winter off the Pacific coast of Costa Rica and Panama. Songs were collected in Costa Rica from a fixed station (September-November 2016) and opportunistically in Panama (August 2007-2015, 2017) using a variety of recordings systems. The results indicate that the pace of whale song change in Panamanian whales is gradual, reaching a new song in 2015. Interestingly, this new song (or any theme) was not present in 2017. To fill up the gap between 2015 and 2017 in Panama we analyzed whale songs recorded in 2016 in Costa Rica, because of the relatively short distance between breeding grounds we assumed connectivity. However, the song recorded in Costa Rica was very different from 2015 and shared only one theme in 2017 with the Panamanian whales, indicating low connectivity at least within a single breeding season. The rapid change in song from 2015 to 2017 in Panama could be due to a high influx of migrant males from other areas. Alternatively, males could have learned a new song during their migration to their breeding ground or even at their feeding grounds. We still do not know where these whales feed nor if they share these areas with other breeding stocks. While this study provides the first documentation of pace of song change for this area, there is a need for long-term acoustic monitoring to better understand the pace at which their songs change to fully understand their dispersal behavior

Key words: cultural transmission, humpback, song,

Introduction

Humpback whales perform one of the most impressive migrations in the animal kingdom, migrating from their high-latitude feeding grounds to their low-latitude breeding grounds, with some of these journeys up to 8300km long (Rasmussen et al., 2007). While at their low-latitude breeding grounds, humpback males will sing their characteristic, complex songs organized in a hierarchical fashion including themes, phrases, and units (Payne & McVay, 1971). During a breeding season, males will generally conform to a specific song type ordering themes in a stereotypic way, even when accounting for individual variation and change over the course of a season (Payne et al., 1983; Payne & Payne, 1985). It is accepted that separate populations will sing distinctive songs, with similarity being associated with the geographic distance between 2 given populations (Winn et al. 1981; Noad et al. 2000). Given this, song similarities spanning ocean basins can give insights into the acoustic contact of the singers with other populations.

To date, the mechanisms of song transmission are not fully understood, yet there are three generally accepted hypotheses: (1) males are moving between breeding grounds inter-seasonally and thus do not display site fidelity (2) males are moving between breeding grounds intra-seasonally (3) songs are transmitted during migration or at feeding grounds (Payne & Guinee, 1983). As documentation of the first two are very rare (Stevick et al. 2013), there is more empirical support for the third hypothesis (Garland et al. 2013a).

Despite debate over the mechanisms of cultural transmission, there is no doubt that it does occur, resulting in change in a song over time. Studies have shown the pace of song change over time is variable, resulting in some themes being present for up to 5 years in a given area while other themes may be unique to one year (Eriksen et al. 2005; Garland et al. 2013b). Noad et al.

(2000) demonstrated the ability of song to completely change in less than two years, displaying rapid song revolution. However, Green et al. (2010) noted that despite humpback song displaying the ability for rapid revolution, there are recurrent patterns within a song that are defined by the “acoustic relationship between adjacent sounds”. Therefore, the authors argue that while units may vary over the course of several years, there are recurrent patterns to how these units are organized.

The aim of this study is to analyze the pace of song change between breeding seasons of the Pacific South American humpback whale population. Understanding the pace of song change will provide insights into possible acoustic contact with other populations, leading to a greater understanding of migratory routes and feeding grounds for this population.

Materials and Methods

I. Breeding Grounds

The breeding ground in Pacific Central America was first discovered in 1995 by Acevedo and Smultea, and constitutes breeding stock G of the IWC. It is unique in that there is evidence of acoustic and genetic overlap of Southern Hemisphere whales with Northern Hemisphere whales (Baker et al. 1993; Baker et al. 1998; Medrano-Gonzalez et al. 2001). Studies have suggested this population of whales feeds in the area surrounding the Antarctic Peninsula and the Magellan Strait (Rasmussen et al. 2004; Acevedo et al. 2007). Although there is currently no observational evidence of feeding ground overlap for the Pacific whales and Atlantic whales that winter in Brazil, there has been an observed report of a whale moving between these 2 breeding grounds (Stevick et al. 2013). This suggests that this population is not isolated, as evidenced by observation and genetic testing. This then infers that acoustic flow could also be transpiring.

II. Study Sites

Recordings for in the breeding ground in the Osa Peninsula, Costa Rica were obtained from a single station deployed at Isla del Caño Biological Reserve (8.715060, -83.870927) at a depth of 25m. At this location, two underwater recorders were used interchangeably from September to November 2016. The recorders used were model: RUDAR-mk2 (Cetacean Research Technology, Inc.) and the SM2M+ (Wildlife Acoustics) Both recorders were programmed to record continuously the soundscape at a sampling rate of 48 kHz during 10-15 days for a total of X recording hours. In Las Islas Secas, Gulf of Chiriquí, Panama (7.993968, -82.029001) recordings were obtained using a variety of recording systems. From 2007-2015 and 2017 recordings were obtained from the boat with a hydrophone and digital recorders. These recordings were obtained while the boat engine was off. In August 2017, we also deployed for 30 days the same SM2M+ model used in Costa Rica at an approximate depth of 25 m and using the same setting described above. 48 kHz. Table 1 shows the total amount of time analyzed for each year.

III. Data Collection

16 total singers were recorded for a total of 64 songs. Recordings were separated by 24 hours in an attempt to minimize sampling the same individual twice and were selected based on the presence of a single singer and relative proximity to the recorder. The recordings from 2010 were of low quality and were discarded. The songs were analyzed visually in Raven 1.5 (2016; Cornell Lab of Ornithology) with a fast Fourier transform size of 2,048 points, an overlap of 50%, and a 512-sample Hann window. Song components were classified into units, phrases, and themes following Payne & McVay (1971). Song units were defined as the smallest continuous sound to the human ear. Phrases were defined as the smallest number of repeated units organized in such a fashion to avoid “lone” units. Themes were defined as grouping of similar phrases. To determine

song change I used the absence of old themes and presence of new themes as a proxy for change. New themes imply both new phrases and new units and is therefore a good representation of overall change. Analysis on the theme level allows for phrases to be technically different from year to year, but still allows for the comparison of similarity between years, highlighting over-all long-term trends as shown in Figure 2. Figure 2 clearly depicts 2 different phrases as evidenced by the inclusion of an additional unit in Fig.2a. However, they both clearly belong to the same theme given the same pattern observed in both years. Therefore, themes were chosen to represent overall change. I calculated the percentage ‘old’ and ‘new’ themes for each year and the accumulative number of new themes over the ten years of data collection. While this approach diminishes individual and intra-seasonal variability, the goal of this study is to examine long-term trends and therefore I feel this action is justified.

Results

A total of 24 distinct themes were identified for males’ songs recorded in Panama, and 4 for Costa Rica (Fig.3). Of the 28 themes identified, 12 were present in more than one year. Themes 1 and 11 were present in four breeding seasons, presenting the longest time a theme was present (Fig.3).

The overall pace of song change for Panama between 2007 and 2017 was 56%, indicating that on average, 56% of the subsequent year consisted of new themes when compared to the prior year. However, the change is not consistent throughout the years. Prior to 2015, the average pace of song change in the Panamanian breeding ground between 2007-2014 was 42.6% (Fig.4). In 2015, a new whale song appears to have been established, and then it changes drastically again in 2017, with no overlap with the 2015 songs. When comparing the 2015 and 2017 Panamanian songs

to songs recorded in the Costa Rican breeding ground in 2016 we found no overlap with the 2015 Panamanian song and only one theme was shared with the 2017 Panamanian song (Fig.3).

Discussion

This study finds that humpback whale males wintering in Panama shift from a relatively gradual change in song structure to an abrupt change in the next two breeding seasons. In addition, we find very little overlap in song structure in the adjacent breeding ground located in Costa Rica. The Pacific Central American region has been experiencing an increasing rate of change in song over the period between 2007 to 2017. The rapid pace of song change overall suggests increased acoustic contact with other populations and does not support the hypothesis these whales are geographically and acoustically isolated. This pace of change is comparable to that cited by Eriksen et al. (2005) in a population in Tonga. The population studied in that article has been shown to “receive” songs from western Australia via cultural transmission in an easterly fashion (Garland et al. 2011).

If a population is isolated, it would follow that the pace of song change over time would be relatively slow. In contrast, if a population were shown to have a higher pace of song change, it could be inferred that this is through contact with other populations, as cultural transmission occurs through vocal learning. Stevick et al. (2004) found that whales photographed migrating from Central America/Ecuador to their wintering grounds near the Antarctic Peninsula had a much higher rate of re-sighting than the Brazilian population, suggesting a relatively high breeding site fidelity in the southern hemisphere whales in the Pacific population. This would suggest that these whales would then be sharing acoustic space either on their migratory routes or on their feeding grounds.

The cause of the increasing rate of change in this area is unknown, although it may be linked to increased acoustic contact with other populations as suggested above. Stevick et al. (2013) also noted an instance of whale moving between Pacific South America and Atlantic South America. This could infer that there are occasional instances of breeding site infidelity, which would assist in explaining the dramatic song shift from 2015 to 2017. Noad et al. (2000) noted that even a small interchange between populations can result in an entirely new song in less than two years. However, these speculations need far more empirical testing before a hypothesis is proposed for the rapid increase in pace of song change in this location.

Passive Acoustic Monitoring (PAM) is essential for population surveys of humpbacks and other larger cetaceans. The ocean represents a difficult “field site” and it is difficult to track these whales over the course of an entire migration. Song similarities imply that populations have recently been in acoustic contact and therefore comparing song similarities between populations is an efficient method in to examine migration routes, breeding site fidelity, and contact with other populations. Therefore, data collected using PAM can be of great value in conservation efforts for these humpbacks. 4 of the 9 distinct population segments for which there was sufficient data were deemed at either moderate to severe risk of extinction (Bettridge et al. 2015). Understanding how these populations are interacting with one another can lead to more comprehensive conservation policies.

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Figures and Tables

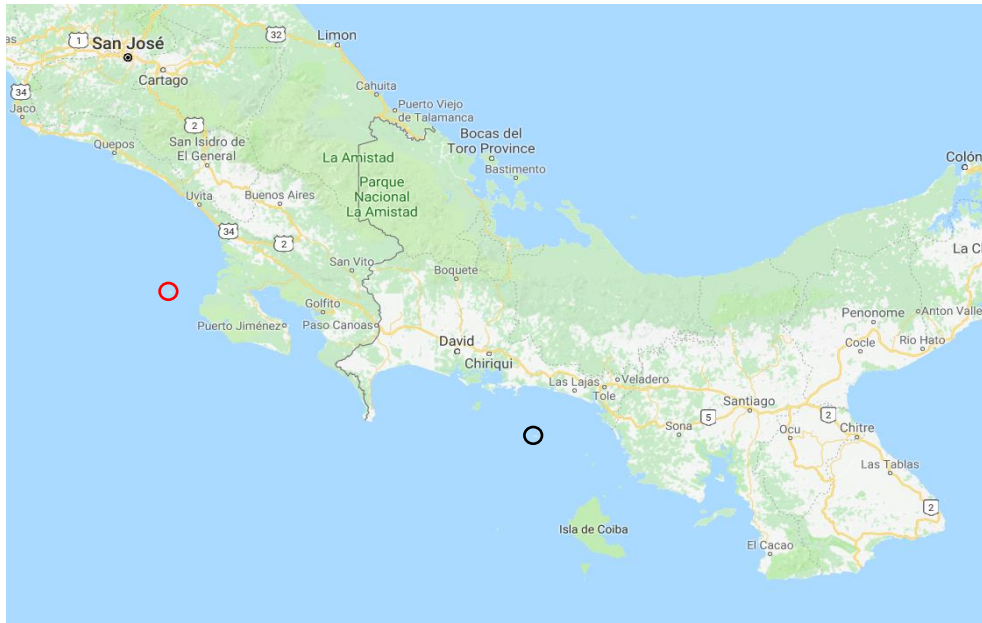
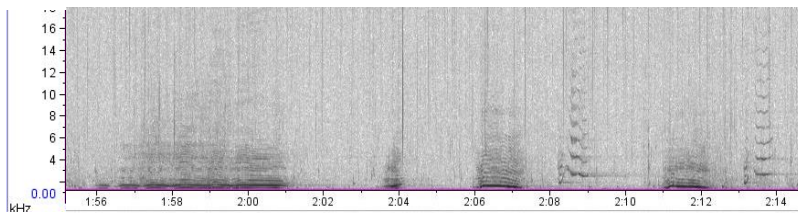


Figure 1. Map indicating the study areas in Costa Rica (red) and Panama (black) in which the recordings for this study were gathered between 2007 and 2017.

a.



b.

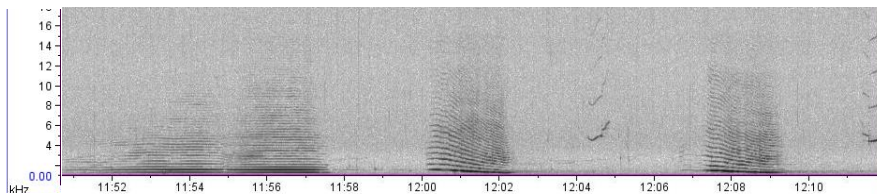


Figure 2. Spectrograms showing phrases from theme 2. a. depicts the phrase from 2007, while b. shows the phrase from 2008.

Themes	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
1											
2											
3											
4											
5											
6											
7											
8											
9											
10											
11											
12											
13											
14											
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17											
18											
19											
20											
21											
22											
23											
24											
25											
26											
27											
28											

Figure 3. Theme types identified in Costa Rica and Panama during breeding seasons of humpback whale (*Megaptera novaeangliae*) from 2007 to 2017. Brightly colored boxes indicate that a theme was present for more than one season while light grey boxes indicate a theme was unique to that year. 2010 has been blacked out as the recordings were of low quality and were not analyzed.

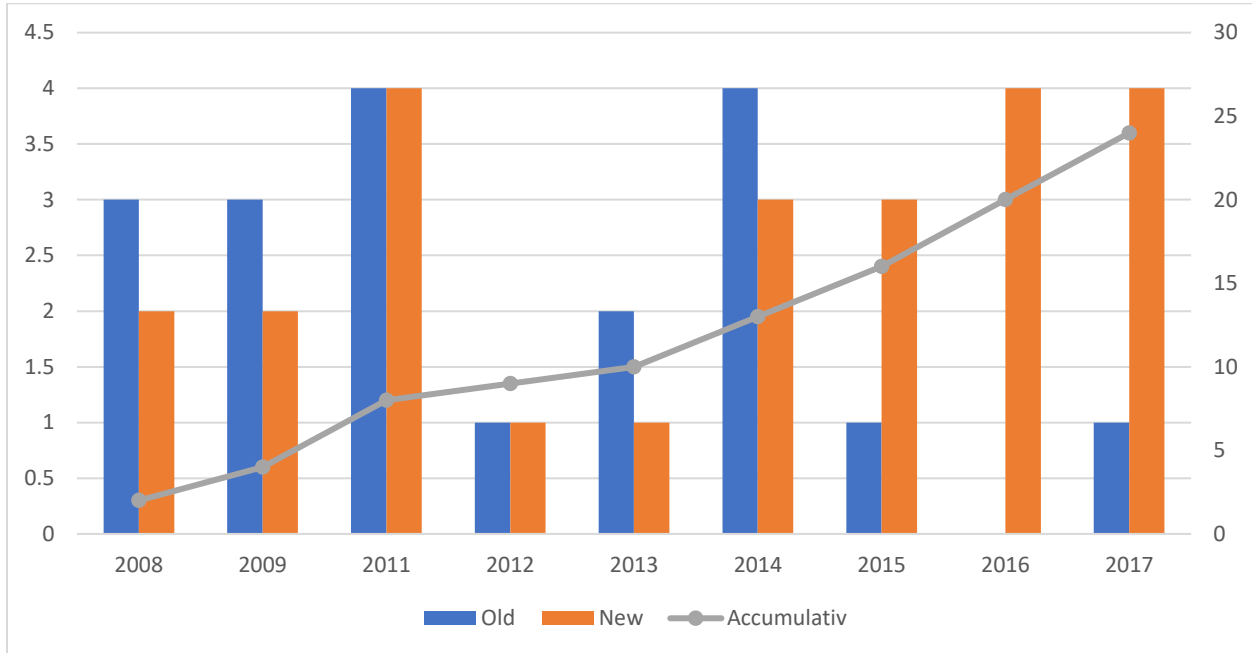


Figure 4. Theme types classified as “old” and “new” for every year. Cumulative number of themes is shown by the gray line. 2007 was not included as it was the first year of recordings.

Table 1. Total minutes of humpback whale recordings analyzed for each year. The recordings from 2010 were of low quality and therefore were not analyzed.

Year	Total Times Analyzed
2007	40
2008	39
2009	54
2010	-
2011	34
2012	9
2013	14
2014	119
2015	111.5
2016	1030
2017	176.5
Total	1,627

Chapter 4: Impacts of Engine Noise on Acoustic Behavior

Abstract

Humpback whales from both the Northern and Southern Hemispheres are known to winter in Central American coastal waters. Their predictable arrival has fueled local whale-watching industry generating concerns about the impact of a growing tour boat fleet in their breeding area. Here we document the acoustic activity of both whales and boats in Caño Island Biological Reserve, Costa Rica between September 2016 and June 2017 using autonomous underwater recorders. Of a total of 160,230 recorded minutes we analyzed 26,995. Our results show a higher incidence of southern humpback whale songs (86%) than of northern whales (<1%) in this area. Southern whale songs were detected in November close to the arrival of North Pacific humpback whales, suggesting a potential temporal overlap between these populations. Southern whales were detected throughout the day, but a significant decline in detection occurred at daytime and particularly at hours of high boat activity. This study provides the first acoustic assessment of habitat use by both humpback whale populations and boat traffic in this breeding ground. Together this information can help local managers and park rangers to evaluate alternatives to protect this breeding area.

PACS number: **43.80Ka**

Keywords: autonomous recorders, communication, cetaceans, ecotourism, song activity.

Introduction

Northern and Southern Hemisphere humpback whales are known to winter off the coast of Central America. North Pacific whales feeding primarily off the coast of California and Oregon migrate to Nicaragua, Costa Rica, and Panama (Steiger et al., 1991; Calambokidis et al., 2000; Rasmussen et al., 1995, 2007, 2012). This whale population is relatively small and shows high site fidelity to both feeding and wintering areas (Calambokidis et al., 2008), which puts them at considerable risk according to the latest review of their status (Bettridge et al., 2015). Southern Hemisphere whales feeding off the Antarctica Peninsula and the Fuegian Archipelago in Chile migrate to Costa Rica and Panama, representing the farthest migration of any mammal (Rasmussen et al., 2007; Acevedo et al., 2017).

The predictable arrival of these whales has fueled the local whale-watching industry generating concerns about the impact of a growing tour boat presence in the region (May-Collado et al., 2017). Studies have shown a negative effect of boat traffic on humpback whale singing activity (Sousa-Lima and Clark, 2008; Sousa et al., 2002). Because singing is an important part of these whales breeding behavior (Payne and McVay, 1971; Tyack, 1981) singing disruption could have long-term impacts on their population viability (Sousa Lima and Clark, 2008).

The Southern Pacific coast of Costa Rica is of great interest because it represents the southern and northern most breeding grounds for North Pacific and Southern Hemisphere humpback whales, respectively. This ecologically unique breeding ground may represent an area of geographical and temporal overlap (Bettridge et al., 2015). Therefore, determining the timing of arrival and departure of these whales in this site is key. The goal of this study is to provide insights on the temporal acoustic occurrence of singing males from both humpback whale populations and

to assess the potential impact of boat traffic, particularly in the form of tour boats that directly target these animals.

Materials and Methods

I. Study Site

Humpback whale songs and boat activity were recorded from September 2016 to June 2017 at a depth of 25m in a location called Jardin (8.719N/-83.863W) within the Caño Island Biological Reserve in the south Pacific coast of Costa Rica using two autonomous recorders (Fig.1). This area has been described as an important part of the breeding ground for both Central America and G breeding whales (e.g., Steiger et al., 1991; Calambokidis et al., 2000; Rasmussen et al., 2007, 2012). It is important to note that Southern Hemisphere whales are reported by tour operators to arrive sometimes as early as July to this area, thus our study is capturing only part of their acoustic activity.

II. Recording and analysis

The recorders used were SM2M+ (Sampling rate: 4-96 kHz -165dB re:1V/uPa) from Wildlife Acoustics (www.wildlifeacoustics.com) and RUDAR-mK2 (Sampling rate up to 96kHz -169dB re:1V/uPa) from Cetacean Research Technology (www.cetaceanresearch.com). They were used interchangeably to reduce field costs and maximize recording time. Both recorders were programmed to continuously record the soundscape in segments of 30 minutes at sampling rate of 44 kHz and 16 bits. Of the 160,230 minutes recorded we selected a 1-min sample every five minutes and uploaded the samples into ARBIMON II an online platform for acoustic cataloguing and inspection (<https://arbimon.sieve-analytics.com>). Recording effort per month is described in Table 1. Each 1-min recording was visually inspected in the spectrogram (Fig. 1) and by scoring presence of whales/boats as 1 and their absence as 0. All song detections, including those perceived as far away, were included in the matrix. We calculated the proportion of 1-min samples with

humpback whale songs and boats by month, time of the day, and recorder model given the possible differences in detection range. We used park ranger records provided by Department of Wildlife Protected areas in Osa to determine the activity of the boats detected throughout the day. A simple regression analysis was used to determine if the proportion of detected song was dependent on boat detections throughout the day.

Results

Southern Hemisphere humpback whale song incidence was 86% with a peak of song detection in October and November (Table 2). In contrast, Northern humpback whale song incidence was less than 1% with song detection happening in December and March. Southern humpback whales were acoustically active throughout the day. However, there is a noticeable decline in song detection during daytime and two ‘shallow’ declines at night. A similar pattern of daily activities was shown by both types of recorders (Fig. 2). Boat activity varied slightly by month with most of the activity happening between 8 a.m. and 4 p.m. This boat activity was attributed to tour boats based on the park ranger registry records. Boat activity after 5 p.m. was attributed to fishing boats known to anchor near the island at night (Table 2, Fig. 2).

The decline in the proportion of whale song detections may be in response to boat presence. We find that 58% of the variation in whale song detection was explained by boat presence ($F=29.8$, $df=1$, $p<0.0001$). This pattern persisted after accounting for variations in month and recorder. Alternatively, whale decline could be the result of whales singing less during the day independently of boat presence. We addressed this possibility by splitting the data into whale detections when boats were present and absent. We find that in the absence of boats the proportion of whale song detections throughout the day is relatively ‘stable’ with a slight decrease between 4 a.m. and 1 p.m. (Fig. 3). In the presence of boats there is a sharp decline in the proportion of whale

detections between 7 a.m. to 4 p.m. Boats arriving time is around 7 a.m. and departure is around 4 p.m. Another decline in the proportion of whale detections happened at 6 p.m., coinciding with a peak of detection of fishing boats.

Discussion

Our study shows that the incidence of humpback whale songs at Caño Island Biological Reserve is higher for Southern Hemisphere whales than for North Pacific whales. The arrival of Southern humpback whales is reported by tour operators as early as July and are often presumed gone by the end of October. While we were unable to deploy our recorder at the onset of the breeding season we showed that these whales are still present in October and early November. Unfortunately, due to hurricane Otto, which affected the South Pacific coast and other parts of the country in November 2016, we could not recover and redeploy the recorder until early December, by that time the Southern whales were gone. It is not until the second week of December that we detected a few humpback whale songs far away from the recorder, and given the timing we assumed these songs belong to North Pacific whales.

Medrano-Gonzalez et al. (2001) has provided evidence for gene flow between these populations, and more recently Jackson et al. (2014) has found that gene flow is slightly higher from Northern Hemisphere to the Southern Hemisphere than vice versa. In this study we provide a timeline of detections that suggest the month of November as the time in which this temporal overlap may be occurring. However, given the small number of North Pacific whale song detections it is likely that if such overlap occurs it involves a few animals.

Southern humpback whales were acoustically active 24/7, however, we noted a decline in the proportion of recordings with whale songs during daytime. This decline appears to be in part natural and in part due to boat traffic (see Fig. 3). We find boat presence explained a significant

amount of the variation in whale singing. Specifically, we observed a decline in whale singing when tour boats are active during the day (8 a.m. to 4 p.m.) and at night when fishing boats are present (6p.m.). Other studies have also found similar patterns in humpback whale singing behavior (Corkeron, 1995; Scheidat et al., 2004; Sousa-Lima and Clark, 2008). For example, Sousa-Lima and Clark (2008) found that the strongest predictor of the number of humpback whales singing in the Abrolhos National Marine Park in Brazil was the number of acoustic boat events recorded, with more boats resulting in fewer whales singing. In the absence of boat noise level estimations and whale location with respect to the recorder we cannot make specific inferences about the effects of boats on the singing whales. However, humpback whales have been shown to decrease singing activity in response to unwanted noises sources as far as 200 km (Risch et al., 2012). Given that several cetacean species are known to respond acoustically to boat traffic and its associated noise (e.g., Erbe, 2002; Nowacek et al., 2007; Weilgart, 2007) it is not surprising that humpback whales in this area of high tour boat activity are responding to it as well.

Conclusions

The discovery of humpback whales breeding in Central American waters was made by Steiger et al. (1991) near our study site describing the presence of North Pacific humpback whales. This breeding population is referred to as the Central American breeding stock and consists of approximately 500 animals (Calambokidis et al., 2008). The latest conservation review has deemed them as a high conservation risk (Bettridge et al., 2015). Our findings show a very low song incidence which might hint at a decline in the use of this site by Northern whales. In contrast, Southern whales showed a high acoustic presence, but they may be facing challenges as the tour boat presence continues to increase in this breeding area. Together this information should help local managers and park rangers to evaluate alternatives to protect this breeding area.

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Figures and Tables

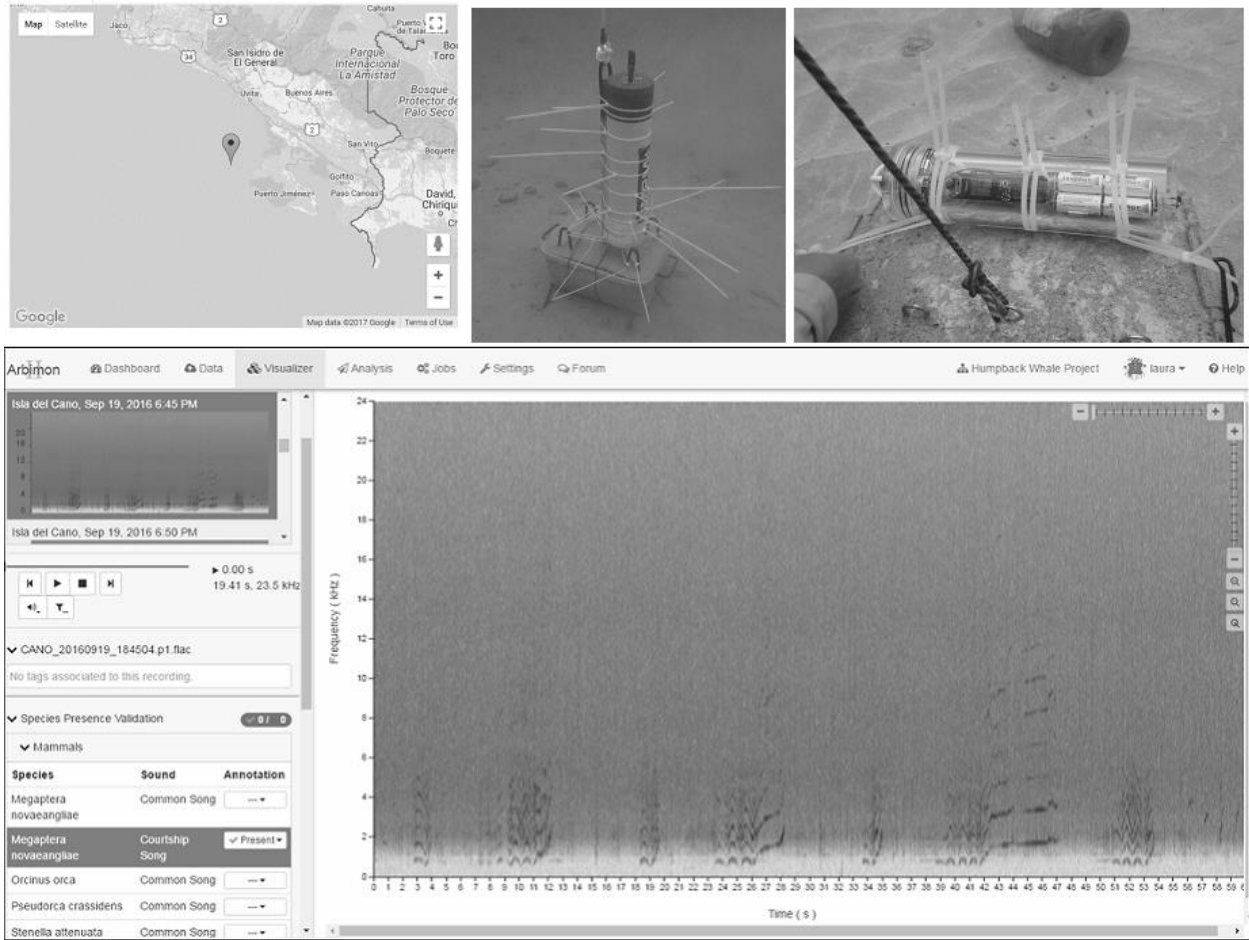


Figure 1. Study area located at 8.719N/-83.863W in the south Pacific coast of Costa Rica. Two recorder models were deployed SM2M+ (top center) and RUDAR-mk2 (top left). Recorders were then uploaded to the ARBIMON II online platform for cataloguing and inspection as shown.

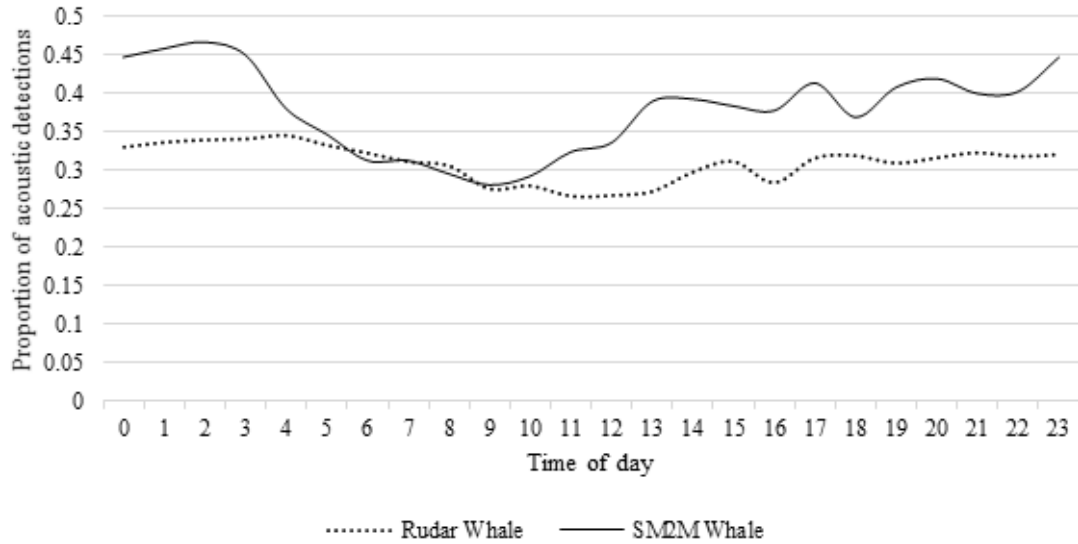


Figure 2. Distribution of the proportion of acoustic detections for Southern Hemisphere humpback whale songs by recorder model throughout the day by recorder (SM2M=September 19 to October 4; RUDAR= October 4-14, October 24 to November 6).

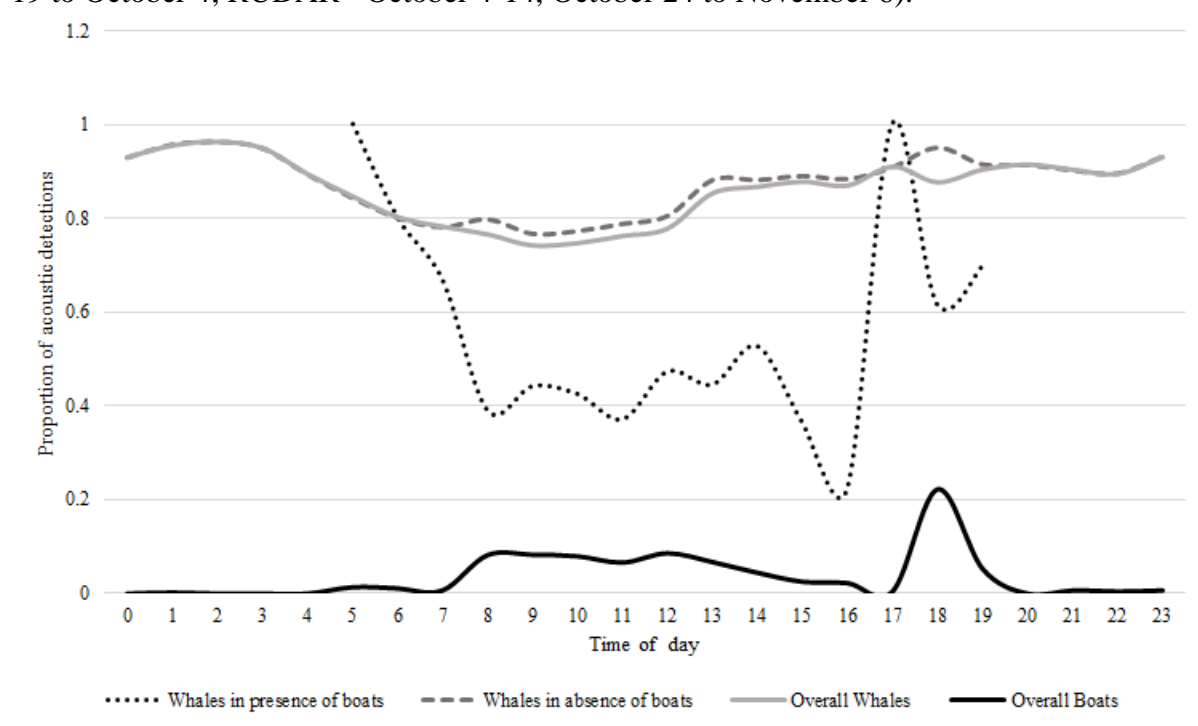


Figure 3. Distribution of the proportion of acoustic detections for Southern Hemisphere humpback whale songs and boats. The figure also shows the proportion of song detections in recordings with and without present.

Table 1. Total number of minutes recorded and analyzed per sampling period and recorder model.

Recorder	Recording Dates	Total time recorded (min)	No. 1-min samples analyzed
SM2M+	September 19 to October 4, 2016	24,910	4,236
	January 12-27, 2017	20,910	4,176
		45,820	8,412
Rudar-mk2	October 4 to14, 2016	14,600	2,733
	October 24 to November 6, 2016	17,540	3,352
	December 6-17, 2016	17,880	3,547
	February 7-18, 2017	16,120	3,189
	March 21- 31, 2017	16,110	3,034
	April 20-30, 2017	16,230	1,607
	June 19-25, 2017	15,930	1,121
		114,410	18,583
Total		160,230	26,995

Table 2. Proportion of cetacean and boat acoustic detections per month and year. The months from September to November contain whale songs from the Southern Hemisphere and from December to March from the Northern Hemisphere (ND=no detections).

	2016				2017				
	September	October	November	December	January	February	March	April	June
No. minutes analyzed	3,240	5,835	1,246	3,547	4,176	3,185	3,034	1,607	1,121
No. Song detections	2,370	5,405	1,140	25	ND	ND	10	ND	ND
Song presence	73%	92%	91%	<1%	ND	ND	<1%	ND	ND
No. Boat detections	184	146	49	172	143	83	117	14	23
Boat presence	5.6%	2.5%	4.0%	4.8%	3.4%	2.6%	4.0%	1.0%	2.0%

Chapter 5: Conclusions and Significance

Reflections and Future Work

Chapter 2 offered an opportunity to expand and refine the stereotypical classification guidelines. The song description of 2016 in Costa Rica provided further support for the conclusions suggested by Payne et al. (1983): that songs evolve within breeding seasons and vary between individuals. In the future, I would like to explore individual variation, as this was not quantified for the purposes of this study. Understanding variability, and quantifying it, on the individual level would allow the scientific community to more fully understand song evolution and cultural transmission. It is also important to acknowledge that boat tour operators have reported whales in this breeding ground as early as July and therefore my study does not encompass the total breeding season, merely the peak months. Therefore, future studies should endeavor to capture an entire breeding season.

Chapter 3 showed that there was a rapid pace of change in the breeding song of the Pacific Central American region. However, to properly characterize the pace of song change, multiple full songs must be analyzed from every year in the study. Since most recordings from every year before 2015 did not have full songs, it is possible that the rate of change was subject to error due to sampling bias. The analysis between years was not made using the further developed classification guidelines described in Chapter 2, given the absence of multiple full songs for each year. Therefore, the establishment of themes was based on similarity alone and therefore is subjected to observer bias. In future studies relating to this topic, obtaining high quality full songs from multiple individuals every year should be the top priority. With full songs, more analysis can also be done, such as the proportion of song dedicated to a certain theme or phrase, for example, and the use of less-subjective modes of analysis, as described in Chapter 2. This second-tier analysis was not able

to be accomplished for this study, due to the absence of multiple full songs for every year, which I acknowledge is a shortcoming of Chapter 3.

In reference to Chapter 4, the impacts of engine noise on acoustic behavior, evidence was shown to support the hypothesis that humpback whales reduce their rates of singing in the presence of engine noise. However, these data could have been made even more impactful through the use of 2 other recorders in different locations to triangulate the locations of the whale and boat in reference to one another. Without these data it is impossible to suggest that these boats were directly masking the songs of the whales, which would have provided a more in-depth analysis of the effects of engine noise on humpback acoustics. For future studies, the ability to locate both the boat and whale would be necessary to establish and quantify the effects of masking on the songs of humpbacks.

There is always future work to be done to strengthen hypotheses. The more work that is done, the more precise and effective conservation policy can be. Therefore, the following suggestions are made to improve the studies presented in this thesis: (1) explore and quantify individual song variability (2) obtain multiple high-quality full songs spanning the entirety of the breeding season to properly characterize the rate of song change over time (3) use 2 other recorders to triangulate the locations of the whales and boats to establish and quantify the masking potential of engine noise.

Significance and Conservation

This study provides the first description of the breeding song of Pacific Costa Rica in 2016 as well as quantifies the pace of song change in Pacific Central America over the period of 2007-2017. This thesis also suggests that humpback whales are significantly more quiet in the presence of engine noise, demonstrating an anthropogenic threat to this population.

The studies conducted in this thesis could potentially be used in cross comparative studies to examine the similarity between the songs of this region and others. This could allow scientists a more in-depth analysis of migratory patterns and population overlap, which is important in constructing effective conservation policy. Understanding if and how distinct whale populations interact with one another is crucial for the development of effective policy and ultimately the conservation of this species. Examining the impact of engine noise on the acoustic behavior of these whales is also critical for the protection of this species. Since singing has been demonstrated to be an important part of the breeding behavior of these whales, the interruption of singing by engine noise could have negative long-term impacts on the viability of the population.

All of the data used in this thesis was collected using Passive Acoustic Monitoring (PAM) devices and demonstrates that PAM is an effective and cheap method to collect data in an aquatic environment. The range of humpbacks and other large cetaceans as well as the difficulty of conducting observational studies in an oceanic environment makes PAM an excellent resource for cetologists and other conservationists to gather large amounts of quality data.

Improving data collection methods using technology such as PAM is important for the future conservation of humpbacks as well as other cetaceans. Gathering quality data allows scientists to create effective conservation policies to preserve this species.

Education

This thesis has suggested that whales are more quiet in the presence of engine noise, representing a threat to these animals. As eco-tourism grows as an industry, it is becomingly increasingly more vital to educate those involved on ethical and eco-friendly business practices. For example, the tour-boat drivers should be educated to keep an appropriate distance from the whales (100m) and to not leap-frog (i.e. cutting off a whale) a traveling pod of whales. Eco-friendly

policy would also ideally limit the hours that a boat could spend following whales as well as the number of boats themselves to reduce noise pollution in the aquatic environment. Larger ship captains, such as the shrimp trawlers or cargo vessels, should also be educated regarding highly-populated areas and reduce their travelling speeds while in these areas. This will assist in minimizing collisions thus decreasing the mortality of these whales and other large cetaceans. Small steps, such as this, would reduce the direct threats to these animals as well as the degradation of their marine habitats.

Resumen en español

Este resumen está dedicado a las personas de Costa Rica y Panamá para preservar la ciencia en su lengua de origen

La ballena jorobada es una criatura magnífica que recorre el trayecto migratorio más largo del mundo desde las áreas de alimentación en latitudes altas hasta las áreas de apareamiento en latitudes bajas. Esta tesis se enfoca en la población de ballenas que se alimentan en las aguas de la Antártida y se aparean en las aguas de las costas pacíficas de Costa Rica y Panamá. En el capítulo 2, se describió la canción típica del año 2016 en Costa Rica. Esta canción tuvo 14 frases y 4 temas distintos. La canción cambió durante la temporada, un fenómeno típico en las ballenas jorobadas. En el capítulo 3, se explicó que durante el periodo de 2007 hasta 2017, el paso de cambio de la canción se incrementó. Este hecho sugiere que esta población de ballenas no está aislada. En el capítulo 4, se demostró que, en la presencia de los barcos, las ballenas cantan menos. En los países que tienen ecoturismo, la educación sobre los métodos responsables de operar barcos en un área de apareamiento es muy importante para preservar la especie. Los países que tengan ballenas en sus aguas tienen la responsabilidad de protegerlas contra las amenazas antropogénicas.

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